

## ON THE MORPHOLOGY OF PALAEOZOIC DIPLOPODS

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### SYNOPSIS

The most comprehensive study of palaeozoic millipedes was published by Fritsch in 1899. More recent authors derived their ideas chiefly from his work and copied his figures. There was and still is a more or less general opinion that most of these millipedes of later palaeozoic times were so different that there is no basis for a discussion of potential relationships with recent taxa. On the other hand the present author is convinced that at least some of the better known recent higher taxa can be traced back to late palaeozoic times. To resolve this apparent contradiction a re-examination of the palaeontological objects and of the status of recent forms was carried out.

The main results show that the differences between the late palaeozoic representatives and recent taxa are due to change of habitats. There is much evidence that the fossil forms lived mainly on the surface, especially on plants; this explains the presence of larger eyes in some groups, the occurrence of bifurcated spines, and the special condition of the exoskeleton (free tergites, pleurites, sternites). Perhaps, as the insects evolved, most millipedes were reduced to hypogaic habitats (under stones, in rotten wood and mould). This change of habitat induced the formation of more rigid exoskeletons (Verhoeff: *Einschubzylinder*), the reduction of eyes, spines, etc.

But the original condition still seems to be preserved in the special structures of some groups (e.g. *Polydesmida*, *Spirobolida*, *Spirostreptida*), occurring only temporarily when animals are moulting. In this stage their exoskeleton becomes divided into sclerites strikingly similar to those of late palaeozoic representatives. The transitory occurrence of these archaic structures seems due to changed functions: they are still useful when moulting necessitates a flexible, extensible exuvium.

### INTRODUCTION AND PRESENT SITUATION

Fossil millipedes are still insufficiently known. Therefore there has been practically no opportunity of using data derived from the fossil record in order to clarify questions of phylogeny. Indeed, with many fossils, even at present, we encounter severe difficulties in establishing a relation with any recent taxon.

There are several reasons for this situation:

(a) The fossil record now available is not very extensive and covers only few formations: most fossil remains originate from Upper Carboniferous deposits and from the Baltic Amber (Oligocene). At all times there must have been little chance of fossilization—perhaps with the exception of the Upper Carboniferous of Central Bohemia.

(b) In many cases the fossils are only moderately or even badly preserved; this precludes detailed statements on their morphology. Fortunately the most comprehensive fossil fauna we know, which was discovered in the so-called "gas-coal" of Central Bohemia, also contains a high proportion of exceptionally well preserved specimens, with microsculpture, ozopores, etc., still visible. But even this seems an insufficient basis for phylogenetic judgements, as the systematics of recent taxa is primarily based on more cryptic details (such as the structure of the gnathochilarium, gonopods, etc.), and not so much on general habitus-characters. Herein lies the main difficulty of determining the systematic position of palaeozoic remains.

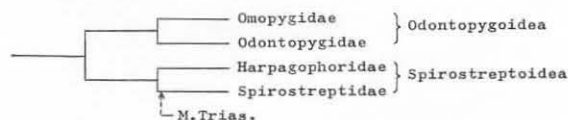
(c) Another point of view has already been emphasized by Hoffman (1969: 575): "Virtually the sum of our present knowledge of fossil myriapods stems from the early work of S. H. Scudder during the 1880's and of Anton Fritsch about a decade later". Although additional remains were discovered and described by several later workers, the classic material, especially of the Fritsch collections, was never studied again. Therefore later authors (such as Verhoeff, 1926; Hoffman, 1969) really had to derive their conclusions chiefly from the old original literature.

Of special note is the attempt of Fritsch (1899) to reconstruct the different types of late palaeozoic representatives and to establish relations with recent groups. He remarks (1899: 43): "Im allgemeinen kam ich zu der Ueberzeugung, dass die weite Trennung der fossilen palaeozoischen Myriopoden von den jetzt lebenden allzu gezwungen ist und schon damals Uebergänge zu den recenten vorhanden waren."—On the other hand, Verhoeff (cf. 1926: 330–359) was opposed to Fritsch's ideas, and so he helped to create the impression that many of these palaeozoic representatives were so different in organization from recent ones that discussions on relationships with present taxa might be more or less useless.

But this seems contradicted by arguments indicating a relatively high phylogenetic age of at least some recent taxa of higher rank. The arguments are chiefly derived from zoogeographical patterns. There are several families (e.g. Rhinocricidae, Spirostreptidae and Platyrhacidae) which occur in different continents, so that Carl (1914) termed this type of discontinuity "transoceanisch". It seems at least imaginable that such distributions might be the results of continental drift. But it must be emphasized that such thoughts—without further arguments—remain pure speculation. But for at least one group with higher categorical rank, the spirostreptomorph diplopods, such additional arguments seem to exist. The relationships of its subtaxa are considered as follows (for

detailed reasoning, based on the principles of Hennig's "Phylogenetische Systematik" (1966), see Kraus (1964, 1966).

For the Spirostreptidae it seems possible to estimate the minimum age of this family. Its representatives occur in the Neotropical as well as in the Ethiopian region (Madagassic subregion included). This is a distributional pattern, still preserved, which can be traced back to Middle Triassic times, when both continents had nearly identical saurian faunas (Colbert; Romer (in Mayr, 1952)). In the sense of a *terminus post quem non* it is concluded that the family Spirostreptidae is at least as old as the Middle Triassic (this concerns the family Harpagophoridae as well, for they form the sister-group of Spirostreptidae).



So, the superfamilies Spirostreptoidea and Odontopygoidea must have originated even earlier, perhaps in late palaeozoic times. To some extent this calculation bridges the enormous gap between recent forms and Upper Carboniferous faunas.

In the light of such considerations the original ideas of Fritsch seem more probable, i.e. the concept of a continuous development from Late Carboniferous forms to recent taxa. This necessitates a re-investigation of the classic fossil material. I had the opportunity to see and to work on Fritsch's originals from Central Bohemia, and to include additional specimens from the Národní Museum v. Praze. For comparison I had fossil diplopods from carboniferous deposits in England before me (collections of the British Museum of Natural History).

#### THE EXOSKELETON OF PALAEOZOIC DIPLOPODA

It is not possible and perhaps not even necessary to report here our results on the structures of fossil diplopods in detail. This will be the object of a later contribution chiefly revising the material from Bohemia. Therefore, the most important characteristics of these palaeozoic representatives are mentioned here in principle.

(a) Larger compound eyes (Fig. 1) evidently occurred more frequently than in present forms. With certainty this was the case not only in the so-called "Archipolypoda" (with the most important genera *Acantherpestes* and *Euphoberia*), but also in the Bohemian forms *Isojulus marginatus*, *I. constans*, *Pleurojulus biornatus*, and in the genus

*Glomeropsis*; one eye of *G. ovalis* was composed of approximately 1000 single eyes. Perhaps the more frequent occurrence of large eyes may be regarded as a basic feature, as in many other "old" arthropods.

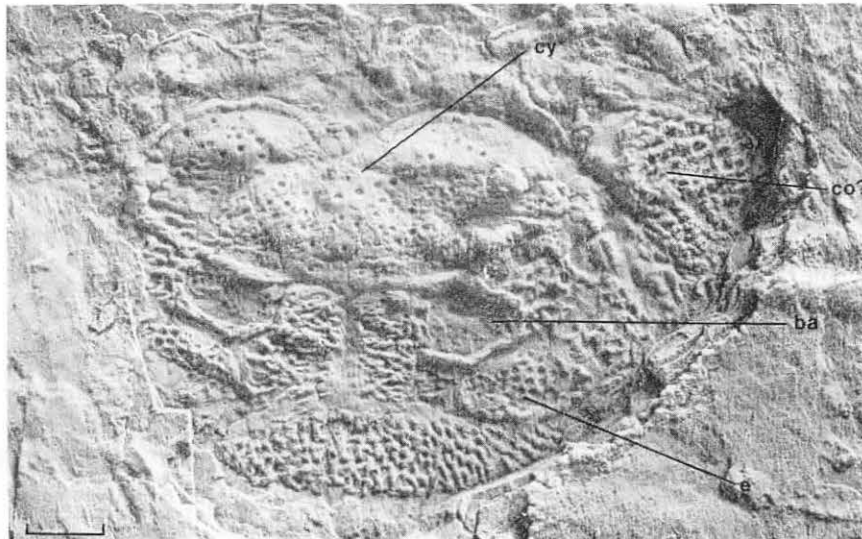


FIG. 1. *Acantherpestes* sp. from Nýran, Bohemia, Upper Carboniferous. Head from in front (ba: base of antenna; co?: perhaps lateral end of collum; cy: clypeus; e: eye). Scale: 1 mm.

(b) In late palaeozoic faunas from Europe and North America we find a considerable number of large forms (Fig. 3) which, on their tergites, were armed with conspicuous spines (as *Euphoberia*, *Acantherpestes*). The largest specimen of *Acantherpestes* known to me had a total length of 235 mm. It seems remarkable that these giants must have had such a weak exoskeleton (Fig. 2). This is demonstrated by the Bohemian fossils which in most cases are much more fragmented and disintegrated than the hard parts of other representatives, especially of those with a more julomorph habitus.

The strange and strong spines on the tergites of the metazonites are the best known feature of the "Archipolypoda". They were arranged in (usually four) longitudinal rows, and often bifurcated at the end. In many cases these spines were broken off during the process of fossilization, but their bases on the tergites always remain visible as rounded depressions.

There are no recent diplopods directly comparable with these spined forms. Only Loomis & Hoffman (1962) described two polydesmoid genera also with forked spines. The few species belonging to this group are comparatively small, probably nothing more than a superficial analogy.



FIG. 2. *Acantherpestes vicinus* Fritsch from Nýřan, Bohemia, Upper Carboniferous. Body segments, lateral view: the head of the animal would be at right (bl: base of leg; s: base of spine; st: stigma in the middle of a pleurite; tg: tergite). Scale: 2 mm.

(c) In most recent diplopods the diplosomites appear as homogeneous rings. The two tergites, two pairs of pleurites and two sternites, which form the original components of the exoskeleton, are completely fused to what was called "Einschubzylinder" by Verhoeff. Diplotergites, discrete diplopleurites and discrete sternites are chiefly confined to the



FIG. 3. *Euphoberia ferox* Salter from Coseley (Staffs.), England, Carboniferous. Body segments, dorsal view; the head of the animal would be at left (bd: base of a spine of the paramedian series; fl: forked spine of the lateral series). Scale: 10 mm.



Oniscomorpha and to a part of the Colobognatha (also Pselaphognatha). Apart from the Oniscomorpha one may say that those present forms with free pleurites, etc., belong to small groups containing few species which themselves are rarely dominant in terms of numbers of individuals.

In contrast to this it seems evident that in Late Carboniferous faunas we had considerably more representatives with free pleurites and/or sternites. I was able to confirm that the species of the archipolypod



FIG. 4. *Pleurojulus levis* Fritsch from Nýran, Bohemia, Upper Carboniferous. Whole animal in lateral position with diplopleurites visible (original in Fritsch, 1899, Pl. 141, Fig. 6). Scale: 10 mm.

genus *Acantherpestes* had discrete sternites (Fig. 2), each of them with paired lateral stigmata; but I could not find any trace of free pleurites, and it seems now that they really did not exist. In the genus *Pleurojulus* we find discrete diplopleurites (Fig. 4), and perhaps the same situation was true in *Anthracojulus*. In the case of *Pleurojulus* Hoffman (1969: 595) thought that the "so-called" 'pleurites' are clearly nothing more than the fractured lower ends of pleurotergites broken when the animal was flattened, not an uncommon occurrence". But I am sure now that these structures cannot be regarded as artefacts.

(d) But we also find other types which seem much more comparable with recent forms. Members of some genera e.g. *Amynilyspes*, *Archiscudderia* and *Glomeropsis* evidently represented the Oniscomorpha (= Pentazonia, = Opisthandria) at this time. Apart from the somewhat strange *Amynilyspes*, which had spines on the tergites, I cannot find characters indicating real differences from recent oniscomorph diplopods. Other types might be termed "julomorph" in their appearance. As in recent forms their diplosomites formed continuous rings ("Einschubzylinder"), as in *Xyloiulus*, *Nyranius*, or *Isojulus*. Hoffman (1969), with reservations, grouped them to spirobolids.

#### BIOLOGICAL INTERPRETATION

It seems possible to interpret the peculiarities of the palaeozoic diplopods mentioned by an analysis of their environment. Representatives of genera such as *Euphoberia* or *Acantherpestes* must have lived on the surface, especially on plants. With their weak exoskeleton and their strong spines these relatively large arthropods must have been unable to burrow in substrates such as rotten wood and mould. Perhaps, as insects evolved, they became more and more restricted to what we may call "underground habitats". At the same time this would explain the tendencies mentioned above (i) towards the reduction of eyes, and (ii) towards more solid diplosomites.

This interpretation is supported by our knowledge of the palaeo-ecological situation, which in Central Bohemia permitted the fossilization of a very rich fauna of carboniferous diplopods. The remains from the Plzeň (= Pilsen) beds were preserved in sediments deposited in lakes, connected by smaller creeks. The diplopods from the coalfield of Kladno-Rakovník (= Kladno-Rakonitz) are embedded in sapropelitic sediments; they accumulated at quiet parts of shallow lake basins. Therefore these diplopods must have lived epigaeically on overhanging vegetation and then fallen into the water. I cannot find any proof for Fritsch's idea (mentioned again by Hoffman (1969: 577))



that at least several of the species of "Archipolypoda" lived aquatically or semiaquatically.

But the original composition of diplosomites (tergites, pleurites, etc.) still seems preserved in some groups (e.g. Polydesmida, Spirobolida, Spirostreptida), occurring temporarily when the animals are moulting. In this stage their exoskeleton becomes divided into sclerites similar to those of late palaeozoic representatives. The transitory occurrence of these archaic structures seems due to changed functions: they are still useful when moulting necessitates a flexible, extensible exuvium.

#### CONCLUSIONS

All arguments favour Fritsch's concept of a continuous development from late palaeozoic diplopods to recent taxa. Striking differences between many of these old forms and present representatives seem due to changed habitats. But despite this better understanding we are still unable to link fossils and recent taxa directly—perhaps this will never be possible.

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#### DISCUSSION

FAIRHURST: I wonder if some of the *Amynilyspedida* could be young stadia of other groups? The one you showed (*Archiscudderia*) could perhaps be a very young archipolypodan; perhaps others could be young stadia of

iuliforms? There is never any mention of life-history stages in the descriptions, yet the order Arynilyspedida is erected on the possession of 15 segments!

KRAUS: It is very difficult to say anything about life-histories. However, in the Bohemian material in which most of the animals are depressed into two dimensions only, the clear view of surface microsculpture enables close comparison of specimens. If they are identical in surface sculpture *and* have approximately the same number of segments, we can conclude they are the same. But this raises another problem—are the remains the animals themselves or their exuvia? Although our present forms eat their exuvia, perhaps, at these times we speak of, they did not.

DOHLE: Are these glomerid-like fossils really oniscomorphs or are they perhaps polydesmoids which resemble glomerids?

KRAUS: I think that forms such as *Glomeropsis* and *Archiscudderia* really were oniscomorph. *Arynilyspes*, which had spines on the tergites, might perhaps be comparable with the oniscomorph polydesmoids.

DOHLE: What arguments lead you to reject the possibility that these Carboniferous forms were aquatic?

KRAUS: Fritsch considered the so-called Archipolypoda to be aquatic because he occasionally found flattened and paddle-like legs. I am now convinced, having carefully observed their legs under the microscope with light coming from above, that they were perfectly normal diplopod legs with a terminal claw and that the flattened appearance is the result of pressure during fossilization.

DOHLE: Are there double sternites in the anterior segments of the exuvia of recent polydesmoids?

KRAUS: I cannot say—the sternites are partly resorbed during moulting. In exuvia of *Orthomorpha* the posterior segments have paired sternites but in *Polydesmus*, in the same order, there are only very reduced vestiges; so there can be much variation.

BÄHR: There are some of these fossil forms that have eyes with about a thousand ocelli. Do these possibly compound eyes occur in other ancient diplopod groups or are they only found in *Glomeris*-like and *Iulus*-like forms?

KRAUS: They occur in *Pleurojulus*, *Isojulus*, and *Glomeropsis* and also in some of the Archipolypoda—the large spined forms. Nothing is known of the detailed structure of the eyes of these palaeozoic forms. I know nothing of fossil *Lithobius*. But even in Trilobites, old Chelicerates and in Aglaspidida there are large complex eyes. Perhaps this character was lost by many of the early arthropod groups when they took to the cryptic habit.

FAIRHURST: I don't remember any of the *Lithobius* fossils having large eyes.